AFTERIMAGES IN THE VISUAL SYSTEM

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AFTERIMAGES IN THE VISUAL SYSTEM

L.T. Zagorul'ko (Leningrad)

The well regulated and coordinated activity of the central nervous system is the result of long adaptation and development and is the sum of the species and individual experience of animals and man. The discovery of the conditioned reflex by I.P. Pavlov and his explanation of this phenomenon as the temporary pathway between active loci of the brain has made it possible to elucidate the mechanism by which nervous coordinations arise. L.A. Orbeli had already long ago (1920-1922) proved his theory that unconditioned reflexes pass through a temporary pathway phase during their initial formation; "the study of conditioned reflexes has shown us the paths which the functional evolution of the nervous system takes; the ready-made coordinational relationships with which we are born were formed over the milleniums, in accordance with the same basic laws which govern the formation of new conditioned coordinational relationships during the weeks and even days and hours, of our individual lives" (L. A. Orbeli). While we may already detect ready-made, stable coordinations imparted by heredity in the lower divisions of the central nervous system, in the activities of the loci which they innervate, something entirely different occurs "in the cerebral cortex, which is the apparatus of in dividual adaptation and is young and free from fixed relationships" (L.A. Orbeli).

Actually, in developing conditioned reflexes, there is a totally unlimited possibility of forming an infinite number of functional

pathways between different sections of the cortex. The process of irradiation of excitatory impulses characterizes the cerebral cortex as a system which is diffuse in the functional sense. Of all the nervous elements, it is the cortical elements in which this functional diffuseness inheres to the greatest degree. Thus, the cortical elements are younger and exhibit functional properties characteristic of early nervous elements to a greater degree than do the cells of other divisions of the central nervous system; by virtue of this, they present unlimited possibilities for individual adaptation. Indeed, during the development of conditioned reflexes (or nervous coordinations), those functional relationships are established under which excitation is propagated through nervous elements (of the cortex) along rigidly defined pathways fixed by the natural conditions of the individual's life or of the laboratory experiment. The ability of the elements of the central nervous system to develop directed, fixed reactions is explained by the intervention of the process of inhibition. Consequently, all coordinated acts effected by the central system reflect a complex functional state characterized by the presence of several simultaneously and sequentially occurring processes; the processes of excitation and inhibition and the courses which they take and the processes of positive and negative and simultaneous and sequential induction.

From this point of view, the study of the activity of human sense organs is of great theoretical and practical interest. On the one hand, it is theoretically interesting to know the physiological mechanisms which govern the development of a strictly determined perception of one or more of a multiplicity of simultaneous external stimuli by the brain. On the other hand, it is of practical importance to know how to remedy the disrupted coordinational activity of the central nervous

system which results from a diseased condition affecting certain sections of the brain.

The teachings of I.M. Sechenov and I.P. Pavlov on the physiology of the brain were further developed in L.A. Orbeli's teachings on the interaction and relationship of afferent systems as applied to man. It was shown in a great number of experiments conducted in the laboratories headed by L.A. Orbeli that there was a definite interaction not only between afferent systems of different modalities, but also within an afferent system itself, as in the case of the cone and rod elements of the retina. Moreover, different components of the same perception enter into definite relationships. These relationships manifest themselves in the form of antagonistic reciprocal relations under certain experimental conditions and in the form of synergetic relations under other experimental conditions.

It is precisely as a result of this that there is no doubt that a certain perception is the result of the activity not only of a certain sense organ, but is also the sum of the extremely complex coordinated activity of several or even many afferent systems. Indeed, we still do not know the specific paths taken by the functional evolution of our perceptions. From this point of view, the principle of the interaction of afferent systems reflects the physiological mechanisms governing a coordinational act in the sensory sphere. The intracentral interaction of afferent systems, as formulated by L.A. Orbeli, is the general principle of the activity of the human brain. Consequently, the study of problems of human higher nervous activity encompasses the investigation of physiological processes occurring in afferent systems not only during the time when a stimulus is acting, but also after it ceases to act and thus reveals the mechanism by which subsequent temporary pathways are formed. Furthermore, it is precisely in the inter-

actions of afferent systems that we must look for the physiological basis of those phenomena which are essentially "conscious" and "subconscious" in psychological terms.

The study of after reactions reveals the laws governing the phase succession of the excited state in afferent systems. From this point of view, the investigation of the interactions of afferent systems in studying visual afterimages has proved to be extremely interesting from a theoretical standpoint and very useful from a practical standpoint. It is well known that the action of a stimulatory agent on a sense organ is accompanied, first of all, by the appearance of a qualitatively determined sensation specific to the sense organ in question, secondly, by the development of after reactions when the stimulus has ceased to act, these being subjectively perceived as afterimages, and thirdly, by remote after reactions of which there is no subjective perception.

The phenomenon of afterimages, known for vision from the time of Peiresc's observations (1634), extends rather widely throughout the activity of human sense organs. Systematic studies, especially of the visual system, began at the time of Purkinje's classic investigations (1825).

A great deal of factual material has now been amassed on the manifestation of the phenomenon with which we are here dealing in other afferent systems.

Thus, Urbantschitsch (1881, 1903) studied after-sounds, Barany (1906, 1907), Abels (1907), and Fischer and Wodak (19[illegible], 192[illegible]; Fischer, [illegible]) described vestibular after-sensations, and Henning (1924), Hofman (1926), and Skramlik (1922, 1926) demonstrated the existence of after-sensations in the regions of the gustatory and olfactory afferent systems.

The study of after-sensations has recently benn carried out on a broad basis in the laboratories headed by L.A. Orbeli. After-sensations in the following afferent systems were investigated: a) visual (Narikashvili, 1944; Volkhov and Zagorul'ko, 1944; Zagorul'ko, 1946, 1947); b) auditory (Arapova and Klass, 1940, 1946; Zagorul'ko and Klass, 1947, Zagorul'ko, Klass, and Federov, 1946); c) vestibular (Zagorul'ko, Komendantov, Osipova, and Entina, 1944, 1947).

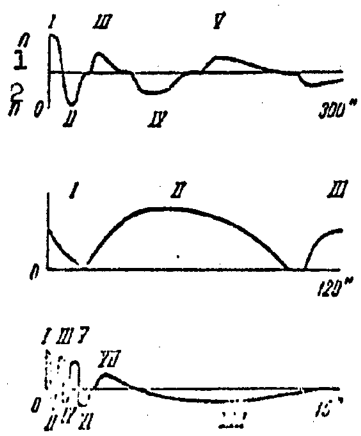

Fig. 1. The development and temporal course of after-sensations; visual (lower, Dittler and Eisenmeier, 1909); auditory (middle, Arapova and Klass, 1940); vestibular (upper, Zagorul'ko, Komendantov, Osipova, and Entina, 1947). Time in seconds is given along the abscissa and the nominal magnitude of the sensation is given along the ordinate. Roman numerals indicate the phases of the after-sensations, P indicates a sensation of turning toward the right, L indicates a sensation of turning the left. 1) P; 2) L.

Certain general physiological characteristics were discovered which were inherent in the after-sensations of all the systems studied and which characterize some of the principal qualities of the activity of the human nervous system, i. e., the periodicity and phase nature of the development and course of after reactions in all afferent systems. In addition, definite individual differences were observed in the development and course of after reactions in different individuals.

It is not difficult to understand that the phenomenon of after-sensation 's an unusual form of the activity of our sense organs. In ordinar day life, these after reactions do not appear; they are inhibite d require certain conditions for their appearance.

On the basis c oretical ideas drawn from contemporary teach-

ings on higher nervous activity, including the physiology of the sense organs, it is possible to make the hypothesis that the development and course of after-sensations reflects the intracentral interaction of peripheral elements of an afferent system which are in different functional states. It may be conjectured that a periodic activity state is developed in the centers of the afferent system as a result of the action of the stimulus, by virtue of inductive interaction between the centers of the excited and unexcited sections of the peripheral apparatus (the retina, cochlea, semicircular canals, etc.).

The course of visual afterimages, as they are observed after the eye is subjected to a moving or unmoving, colored or uncolored stimulus, despite the extraordinary diversity and multiplicity of their characteristics, follows a series of very general, but definite and always manifested, rules. These rules are so constant that there is no doubt that they characterize some of the basic features of the course of physiological processes in the human visual afferent system.

First of all, it is necessary to note (and this can be very important for understanding certain disruptions of higher nervous activity) that there is no strict correspondence between the after-sensations (visual, auditory, et. al.) and the stimuli which cause them.

The periodicity of afterimages (and this holds for all afferent systems) characterizes that course of the after reaction in which perception at times disappears and at times reappears in response to a single stimulation of the eye, this occurring several times over a long period of time. The periodicity of the extinguishment of visual afterimages is characterized by two factors: first, by the development of dark intervals during which there are no after-sensations and, secondly, by the appearance of one or more phases of the after reactions

(Purkinje, 1825; Plateau, 1834; Fechner, 1840; Aubert, 1858, 1865; Bruecke, 1864; Charpentier, 1891, 1896; Hering, 1890; Hess, 1891, 1894, 1901, 1902, 1903, 1920; Bidwell, 1894; Boscha, 1894; Hamaker, 1899; Kries, 1896, 1901; McDougall, 1904-1905; Dittler and Eisenmeier, 1909; Ebbecke, 1920, 1921; Froehlich, 1921, 1921a, 1929; Bayer, 1926; Allen and Dallenbach, 1938).

The intensity and clarity of the afterimages decreases with each phase and the duration of the phases increases as time goes on. Each successive phase has a tendency to fuse into the background and toward the end of this development, they become difficult to distinguish from the surrounding visual field. The dark intervals which separate the phases of the after reactions undergo exactly the same changes in extinguishment. The changes in the phases involve not only their duration, but also the quality of the sensation. This is especially marked when a colored light source is used as the stimulus.

Thus, for example, under the action of a brief light (chromatic or achromatic) stimulus, a very brief dark interval (approximately 0.04 second) occurs immediately after the visual sensation from the action of the light itself has died away and this is followed by the development of Hering's (1909) first positive visual afterimage, this being of the same quality as the object-supplying the stimulus: bright when the stimulus is achromatic and of the same color as the stimulus when the latter is chromatic (Dittler and Eisenmeier, 1909; Orbeli and Dittler, 1910; Froehlich, 1921, 1922, 1929; Bayer, 1926; Vogelsang, 1928; Frehafer, 1929).

After the first positive phase of the Hering afterimage, a second dark interval appears, approximately four times as long as the first (0.16 second).

After the dark interval, the second phase of the visual afterimage -

a Purkinje form – develops (Purkinje, 1825); when the stimulus is uncolored, this image is, as a rule, light blue or grey-blue and, when the stimulus is colored, the image is of approximately the complementary color. Thus, the Purkinje form is complex: it is positive for neutral components and complementary (negative) for colored components; its duration is approximately 0.17- 0.25-0.5 seconds: (Osann, 1833, 1836; Mueller J., 1838; Young, 1872; Davis, 1872,1885; Judd, 1927, Karwoski, 1929; Karwoski and Crook, 1937; Karwoski and Warrener, 1942; Karwoski and Parry, 1943; Murrey, 1943; Narikashvili, 1944; Volkhov and Zagorul'ko, 1944; Zagorul'ko, 1946, 1947).

After the Purkinje form has faded away, there occurs a third dark interval, longer than the second and considerably less distinct, nearly fused with the visual field.

The third phase of the visual afterimage is longer than the second, is considerably less distinct, and toward the end of its development, merges virtually unnoticeably into the background of the surrounding image of the visual field. This image bears the characteristics of the stimulatory light in the quality of the sensation itself: it is bright when the stimulus is uncolored and is always similar in color to a chromatic stimulus, consequently duplicating the first Hering afterimage to a certain degree. This image is called the Hess image and was observed by Boscha (1894), Hamaker (1899), Hess (1900, 1903), Kries (1911), Dittler and Eisenmeier (1909), Muller (1909), and Feinbloom (1938). It lasts for ten seconds. Certain authors such as Hamaker (1899), Froehlich (1921), et al. have described a fourth dark interval, still less distinct and more prolonged, and a fourth visual afterimage of very weak intensity: it is impossible to evaluate the duration of this afterimage, since both its beginning and end are virtually indistinguishable. It is slightly lighter than the background

and has the characteristics of a complementary afterimage.

However, the course of visual afterimages depends on a number of external and internal factors. On the one hand, the intensity, duration, and surface area of the stimulatory object have their effect and, on the other hand, the site at which the retina is stimulated and the functional state of the visual system and of the observer himself exert an influence. Above all, these influences affect the duration of certain images, their intensity (brightness and hue) and clarity, the number of phases in the after reactions, the latent periods of the development of the reactions, etc. As experiments by Aubert (1865), Helmholtz (1866), Judd (1927), Vogelsang (1928), and Suchman and Weld (1938) show, increasing the intensity of the light stimulus is accompanied by an increase in the brightness, saturation, distinctness, and number of phases of the afterimages. The same was shown to hold true when the stimulus was allowed to act for a longer time, by the experiments of Muller (1838), Seguen (1880), Ebbecke (1929), Juhasz (1920). Froehlich (1921a), and Starkiewicz (1939), and when the surface area of the stimulatory object was increased, by the experiments of Juhasz (1920), Froehlich (1925), Velinsky (1924), and Gellhorn and Kuhnlein (1926). Indeed, there exist optimum stimulation conditions above and below which there is a deterioration in the course of the afterimages: according to Helmholtz, 1/3 second is necessary to obtain a positive afterimage; according to Ebbecke, a brief display of light is accompanied by a positive afterimage, while a long display is accompanied by a negative afterimage; according to Juhasz, the duration of the Purkinje form increases from its threshold value until the display time reaches approximately 60 seconds; according to Froehlich (1921), the brightness and duration of an afterimage increases when the duration of illumination is increased, but only when the light display does not

exceed 1-2 seconds, a decrease in brightness and duration and even the development of a negative image occurring at display times longer 2 seconds.

Moreover, an increase in the illumination of the background on which stimulation of the eye is carried out or on which the after-image is observed serves to decrease the intensity of the light stimulus (Juhasz, 1920: Fechner, 1838; Exner, 1868; Froehlich, 1921, 1921a; Ebbecke, 1929; Karwoski, 1929).

The latent period of the development of afterimages undergoes precisely the same changes in magnitude, but within a considerably narrower range.

Kries (1896), P. Muller (1909), and Juhasz (1920) showed that the latent period of a positive image decreases when the intensity, duration, and surface area of the stimulatory object are increased. Creed and Granit (1928), Creed and Harding (1930), and Granit, Hohenthal, and Uoti (1930) showed that the latent period of a negative afterimage increases when the intensity of the light stimulus is increased.

According to the experiments of Hess (1900, 1920), McDougall (1904-1905), Dittler and Eisenmeier (1909), Bayer (1926), and Froehlich, the presence of a different stage of adaptation to light and to dark causes no basic changes in the course of afterimages.

When dark adaptation has been developed, a lesser and lesser intensity of the light stimulus is required to cause afterimages and, consequently, dark adaptation acts in the same fashion as does an increase in the intensity or duration or surface area of the stimulatory object. No basic difference has been detected in the course of afterimages at the periphery and in the center of the retina during light and dark adaptation. This was confirmed by Kries ([illegible], 1905, 1911).

Basically, the course of the afterimages is identical in the regions of central vision and at the periphery of the retina, according to Hess' data (1903, 1904, 1920). The only difference is a slight acceleration of the succession of phases at the periphery of the retina as compared with the center (Woinow, 1895; Klug, 1875; Walter, 1899; Washburn, 1900; et al.). A lesser light stimulus intensity is required at the periphery of the retina than at the center to cause afterimages (Aubert, 1858, 1859; Froehlich, 1921). Kries (1869, 1901, 1902) came to the conclusion that there were no Purkinje afterimages at the periphery of the retina in daylight and there were never any in the central vision regions; red light does not cause a Purkinje image and these forms are consequently a function of the night vision apparatus. However, Kries' data has not been confirmed in experiments by other authors (Hess, 1901, 1903, 1920; Dittler and Eisenmeier, 1909; Froehlich, 1921; et al.).

A deterioration of the course of the visual afterimages also occurs when the visual system or the observer is in a state of fatigue (Froehlich, 1921; Gellhorn and Weidling, 1925).

The individual characteristics of the course of afterimages are related to their hues (Bruecke, 1851; Aubert, 1865; Hilbert, 1893; Berry, 1927; Frehafer, 1929; Markowski and Crook, 1937), the latent period of development and the duration of the image and the number of phases (Franz, 1899, 1900; Munk, 1900; Morsch, 1938; Narikashvili, 1944; Volkhov and Zagorul'ko, 1944).

Parinaud (1882, 1885, 1898), Filhene (1885), Delabarre (1888, 1889), Bocci (1898), Mochi (1910) and Kollner (1916) concluded that visual afterimages are of cerebral origin.

Exner (1884, 1890), Wagner (1896), Katz (1911), and Craik (1940) confirmed, on the basis of their experiments, that the retina is the

site at which afterimages arise.

McDougall (1901) thinks that afterimages are based on the activity of photochemical substances in the retina, while the appearance of a certain portion of their colored constituents is chiefly determined in the cortex.

G.E. Mueller (1930), thinks that positive afterimages are of both retinal and nervous origin, while negative afterimages are of purely nervous origin.

One of the most widely held theories of afterimages originated with Scherffer (1761, 1765) and attempts to explain them by the phenomena of eye fatigue. Fechner (1838) and Helmholtz (1866) suggested that afterimages are partially based on the continued excitation of the retina (after stimulation has ceased) and partially on a decrease in sensitivity (fatigue) of the retinal elements. The authors thus assume that a positive afterimage is a consequence of a still unextinguished excitation of the retina and that a negative afterimage arises as a result of changes in the excitability by light of a retinal site fatigued by prior stimulation; a complementary afterimage does not reflect a state of present activity but, on the contrary, is the result of a decrease in the previously existing internal light. Fick and Gurber (1890) also assumed that positive afterimages are the result of a primary excitation state and that negative afterimages are caused by a decrease in the sensitivity of the retina. Wundt (1910) explains afterimages by three mechanisms: 1) by an excitation process which lasts longer than the action of the stimulus and entails the development of a positive afterimage identical in color to the stimulus; 2) by a change in the excitation state of the retina (as a result of fatigue) which entails the development of a positive or negative complementary afterimage; 3) by contrast, which causes the after-sensation.

to have a greater or lesser intensity.

Lazarev (1918, 1923, 1926), Putter (1920), Judd (1927), and others developed a photochemical theory of visual afterimages.

Herring (1890) and Hess (1891, 1901) explained the negative afterimage by after-contrast rather than by retinal fatigue.

Froehlich (1921, 1921a, 1929), Bayer (1926), and others consider afterimages to be a specific cerebral activity.

The periodicity and phase variation of after reactions has attracted the attention of many others. Thus, for example, Plateau (1834, 1836) suggested that the transition of the retina from an excited state to a quiescent state proceeded in oscillatory fashion, both with respect to time and to spatial relationships; the former is responsible for positive and negative afterimages and the latter causes irradiation phenomena. Charpentier (1896) assumed that there were retinal oscillations taking the form of a lateral vibration of the external segments of the rods and cones at a frequency of 37 oscillations per second. Burch (1913) developed a hypothesis which asserted that each peripheral element is protected from excessive stimulation. by a shunt factor. The cessation of stimulation is accompanied by the liberation of the accumulated energy of a counteraction which ensures that the afterimages are extinguished. Young (1872) suggested that the phases of after reactions manifest themselves during the transmission of nervous impulses from the retina to the brain and from the brain to the retina and thus occur before the excitation process has been completely extinguished. Davis (1872) assumed that when one of the three types of Young-Helmholtz fibers was excited, by analogy with electromagnetic induction excitation was induced in the nerve fibers of the other types, thus producing complementary afterimages. Starkiewicz (1938) proposed an "electrical" theory of afterimages. The

author suggested that there is an intermediate stage between the layers of cones and rods on the one hand, and the nerve fibers on the other, this stage having the characteristics of a physical capacitor which discharges in oscillatory fashion and thus causes extinguishment of the afterimages. Helmholtz (1876) explained the periodicity of visual images by wavering of the attention. Froehlich (1921, 1921a, 1929) and Ebbecke (1921, 1929) saw the periodic extinguishment of afterimages as the manifestation of certain antagonistic processes occurring in the centers.

Thus, on the basis of this outline of theories of visual afterimages, we can to a certain degree elucidate the basic tendencies in this direction which have developed since the time of Scherffer. On the one hand, Th. Young's views (1808), partially developed by Mueller and especially by Helmholtz, led to the creation of the dualistic theory of vision advanced by Voinov, Parinaud, and Kries, to the modern photochemical theories of excitation advanced by Lazarev, Putter, and Hecht, and to the recent investigations by Granit (1944, 1945) and Adrian (1945) which completed our knowledge in the field of the study of the specific activity of the receptors and nerve fibers of the visual afferent system.

However, all attempts to explain visual afterimages by the activity of the receptor elements alone have ended in failure and the subsequent inevitable turning for help to psychological interpretations (wavering of attention, errors in judgement).

On the other hand, the creation of electrical and mechanical schemes to explain the processes and phenomena which take place in the retina during and after its excitation are still less satisfactory in clarifying the extreme complexity of the course of visual sensations and after-sensations. Each of these schemes can be a more or less suc-

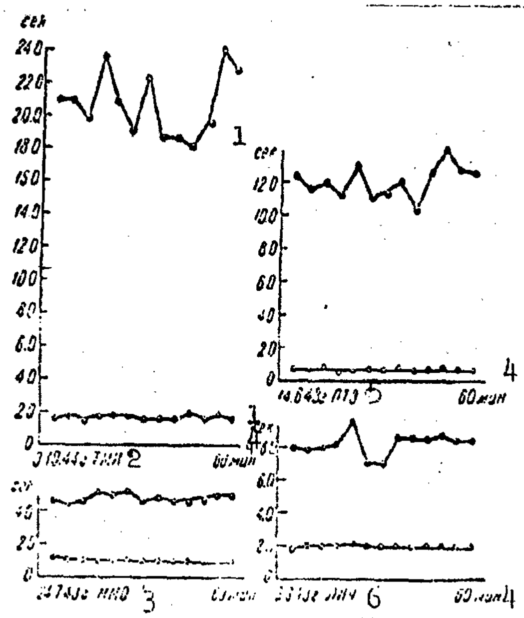

Fig. 2. Curves showing four types of development and course of a Purkinje afterimage. The time of the experiment in minutes is shown on the abscissa and time in seconds is shown along the ordinate. The lower curve is the latent period of image development and the upper is its duration. 1) Sec; 2) g. TMI; 3) g. MMO; 4) min; 5) g. LTZ; 6) g. LNCh.

cessful analogy or model of the phenomena and processes of retinal excitation and may be physical or mechanical schemes describing processes and phenomena already known from other areas of science (the alternating discharges of capacitors, the coiling and uncoiling of a spring). According to the ideas of the authors of these theories, excitation processes and their aftereffects are manifested in one certain limited section of a system, such as in the retina, and it is only these processes which determine the entire complex of phenomena, thus being completely independent of the functional state of the remaining portion of the visual system.

A third tendency, which began with Hering and was carried on

by his students and followers, Hess, Dittler, Froehlich, and to a certain degree, by Ebbecke and Gellhorn, attempts to overcome the limitedness of the theories herein described, using the physiology of the nervous system.

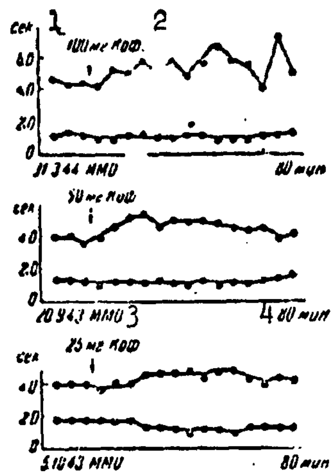

Fig. 3. Curves showing influence of caffeine on course of Purkinje afterimage. Other specifications same as for Fig. 2. 1) Sec; 2) mg. caffeine; 3) MMO; 4) min.

Actually, it is now already insufficient merely to know the organization and activity of the peripheral receptor apparatus in order to understand the entire complexity and subtlety of our sensory reactions. This activity is caused by the functions of all the afferent systems, which include as integral parts the peripheral receptors, the nerves, a whole series of intercalary, intermediate nerve centers, and finally, the cells of the cerebral cortex.

Moreover, the activity of any one afferent system is a result of the functional state of the other afferent systems which interact with it.

From this point of view, the study of the activity of the visual afferent system is thus essentially an investigation of the specific reflex reactions effected by the brain.

Actually, on the basis of our experiments, we have a certain basis for stating that there are four types of course and development of visual afterimages. Type A (Fig. 2, LTZ) is characterized by a short latent period of development and a long after reaction duration;

Type B (Fig. 2, LNCh) is characterized by a long latent period of development and a relatively short afterimage duration; Type C (Fig. 2, MI) is characterized by a long latent period of development and a very long image duration; Type D (Fig. 2, MMO) is characterized by a relatively short latent period of development and a short afterimage duration. The study of the correlation between afterimage course and the types of nervous system which were established in I.P. Pavlov's investigations of higher nervous activity should be rather interesting.

Moreover, the action of such pharmacological agents as caffeine, strychnine, and phenocoll, which possess different degrees of neurotropism, causes a definite change in the development and course of the Hering and Purkinje visual afterimages. As little as 25 mg of pure caffeine administered per os causes a reduction in Purkinje image development time and increases its duration (Fig. 3); the influence of caffeine begins after 7-10 minutes and continues for 40-60 minutes.

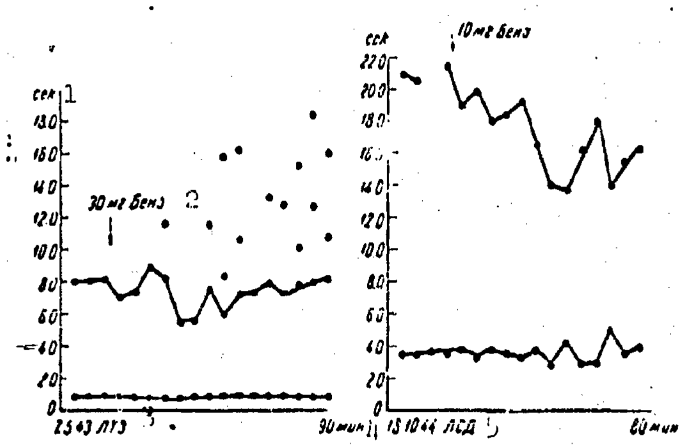

Fig. 4. Curves showing influence of benzedrine on course of Purkinje afterimage. Other specifications the same as for Fig. 2. 1) Sec; 2)mg. benzedrine; 3) LTZ; 4) min; 5) LSD.

On the basis of a number of experiments, we have been given the impression that the nature of the influence of "nerve poisons" depends

not only on the quantity of the drug administered, but also on the type of after reaction. Thus, for example, the Purkinje afterimage decreased in duration in subject LSD (Fig. 4, Type C) after the administration of 10 mg of benzedrine, while its duration either increased or showed no change in other subjects, depending on the nature of the afterimage. Increasing the dosage of benzedrine to 30 mg caused the development of additional waves of afterimages, somewhat unstable in duration, in subject LTZ (Fig. 4); certain subjects manifested this effect at lower dosages. From all the forms of this influence known to us, which depend on the original activity levels of the system in question as has been shown by the school of Academician L. A. Orbeli, we are inclined to believe that the influence of benzedrine is a sympathetic effect. Hypodermic administration of strychnine

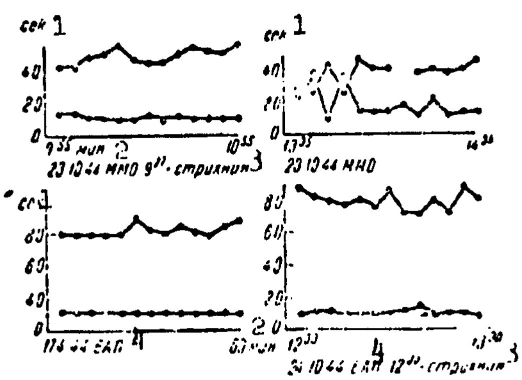

Fig. 5. Curves showing influence of strychnine on course of Purkinje afterimage. Other specifications the same as for Fig. 2. 1) Sec; 2) min; 3) strychnine; 4) YeAP.

is accompanied by a reduction in the development time of the Hering image and by an increase in the duration of the Purkinje image. Fig. 5 shows a sharp increase in the duration of the Purkinje phase in subject YeAP. In MMO (Fig. 5), strychnine caused a distortion of the usual form

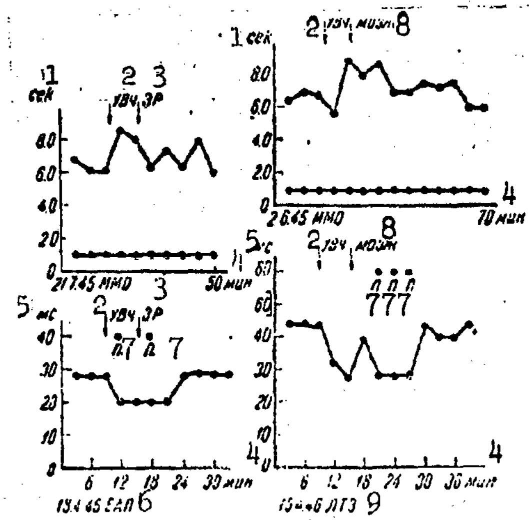

Fig. 6. Curves showing development and course of Hering (lower) and Purkinje (upper) afterimages under the influence of the action of UVh on the visual region of the cortex and on the cerebellum. Time in milliseconds is shown along the ordinate (lower curves). The letter P designates a Purkinje afterimage. The arrows indicate the beginning and end of the light stimulus. The other specifications are the same as for Fig. 2. 1) Sec; 2) UVCh; 3) visual region of cortex; 4) min; 5) μ sec; 6) YeAP; 7) P; 8) cerebellum; 9) LTZ.

of the Purkinje image; rather than a slight increase in duration, a change in the development time and course of the image was noted at the beginning of the dark adaptation period. The latent period of image development exceeded the duration of the image in certain determinations, a phenomenon never observed under normal experimental conditions. Thus, if it is acknowledged that caffeine predominantly affects cortical processes, that strychnine has a diffuse effect on all nervous elements of the visual system, and that benzedrine – an analogue of the sympathetic system – shifts the latter to a different

functional level, by virtue of its adaptational and trophic influence, it then becomes obvious that the development and course of visual afterimages depend on the functional state of the various divisions of the central nervous system (cortical for caffeine and strychnine, subcortical for benzedrine and strychnine). The mechanism of this effect probably reduces to a disruption of the balance between the excitatory and inhibitory processes in the visual afferent system and to a change in the rate at which nervous processes proceed (Zagorul'ko, 1946).

Changes in the chemicity of the cortex caused by hypoxemia, hyperventilation and hypercapnia have a susbtantial influence on the course of the Purkinje image (Volokhov and Zagorul'ko, 1944; Zagorul'ko, 1947).

We subsequently used the method of local excitation of the human brain by a UVCh [uhf] field (Livshits, 1944). The action of UVCh on the visual region of the cortex and on the cerebellum causes a sharp change in the development and course of the Hering (Fig. 6, YeAI and LTZ) and Purkinje (Fig. 6, MMO) images. This change in the images has a different development time when the UVCh field acts on the visual centers and when the cerebellum is irradiated; in the latter case, changes characteristic of the sympathetic effects of the cerebellum develop more slowly. The Hering image undergoes a decrease in development time. In addition, the Purkinje image, lacking under normal experimental conditions, is still present. We tend to consider the appearance of the Purkinje image (designated by the letter P on the diagram) as the result of the involvement of new levels of the central nervous system - the visual afferent system - in the active state. The quantitative change in the Hering image is also accompanied by a qualitative changes: it very often becomes grey- or light-blue and ac-

quires the characteristics of the colored components of the Purkinje image. In both types of effect, the Purkinje afterimage undergoes an increase in duration, which sets in earlier and ends when the visual region is irradiated. Thus, we are given the impression that, first of all, the rate of development of the first Hering phase increases under the influence of UVCh and, secondly, that the rate at which the second Purkinje phase proceeds decreases under this influence. This phenomenon can be understood only from the point of view of the fact that both these phases reflect a change in the functional state of different levels of nervous organization of the visual afferent system. Indeed, this effect was not identically manifested in all subjects; in certain subjects, it was either very slight or even entirely lacking. In subject MMO, irradiation of the region of the cerebellum with UVCh was accompanied by an increase in the duration of the Purkinje image amounting to a factor of 1.5-2, a phenomenon not observed when the visual region was irradiated. Moreover, both types of irradiation produced a change in the quality of sensation; very often, the image increased in brightness or in the number of colored components. The difference in development time of the effects observed when the visual region of the cortex was irradiated and when the cerebellum was irradiated may be an indication of a difference in their origins. On the one hand, we have the immediate change in the functional state of the cortical centers and possibly in the subcortical centers - the visual system- and on the other hand, we have the fact that the visual afferent system is subject to secondary influences arising in the autonomic centers of the cerebellum when the latter is irradiated; this is indicated not only by the slower development of the effects in the latter case, but also by the development of pa[illegible] when the region of the cerebellum was irradiated. On the basis of our

experiments, we may thus speak of the cerebellum as the regulator of the physiological processes which occur in the human visual afferent system.

It seems to us that the change in the course of the afterimages under the influence of focal reorganization of the functional state of the brain by a UVCh field under the conditions of our experiment is in accordance with the data obtained by Vujic and Levi (1939, 1940, 1940a) on the development of visual afterimages in organic and functional disorders of the brain.

The development and course of the Hering (Fig. 7, lower curves) and Purkinje (Fig. 7, upper curves) afterimages are subject to an effect of complex character when a painful stimulus is applied to the skin receptors; in the majority of subjects, a decrease in the development time of the Hering image (Fig. 7, LTZ) and a decrease in the duration of the Purkinje image (Fig. 7, LTZ) was observed in all experiments; in a minority of subjects, an increase in the duration of the Purkinje image (Fig. 7, YeAP) and an increase in the development time of the Hering image (Fig. 7, YeAP) was noted in all experiments. The complexity of this effect is explained by the multiplicity of physiological mechanisms which carry out the effects of pain, including nervous effects, which depend on the type of relationship between the afferent systems and sympathetic and hormonal effects. These data are in accordance with the work previously conducted in the laboratories headed by L.A. Orbeli on the influence of painful stimuli on the sensitivity of certain afferent systems (Zagorul'ko, Lebedinskiy, Turtsayev, 1933; Volokhov and Gershuni, 1937; Durmish'yan, 1937). According to investigations carried out by the school of Academician L.A. Orbeli, the influence of painful stimuli on the course of physiological processes in the various systems of animal and human organisms is uni-

versal. Consequently, the physiological reactions of the human brain also fall under the influence of the effects of painful stimuli.

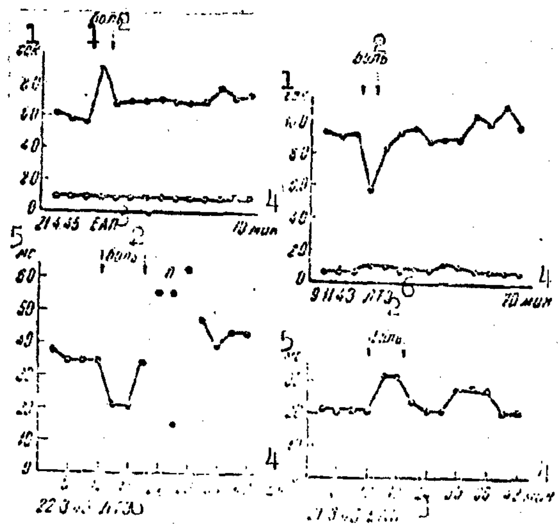

Fig. 7. Curves showing development and course of Hering (lower) and Purkinje (upper) after-images under the influence of painful stimulation of the skin of the hand; arrows indicate beginning and end of painful stimulation. Other specifications the same as for Figs. 2 and 6. 1) Sec; 2) pain; 3) YeAP; 4) min. 5) μ sec; 6) LTZ.

The study of the Hering and Purkinje visual afterimages during their interaction with the processes occurring in the other eye and in afferent systems of other modalities is in complete accordance with the teachings of L.A. Orbeli on the complex nature of our sensations. Sensation is effected not only by the processes which occur in the system in question, but also by processes nonindifferent to it which occur in the other afferent systems. In this respect, according to L.A. Orbeli's concept, many reactions which occur in a certain afferent system and are not subjectively perceived have their influence on the final form of a certain sensation. In addition to the inter-

action of subjectively perceived reactions, nonperceived reactions have their effect on the everyday activity of our sense organs and on our higher psychic functions through a great multiplicity of factors and we are still far from a complete knowledge of this area of investigation.

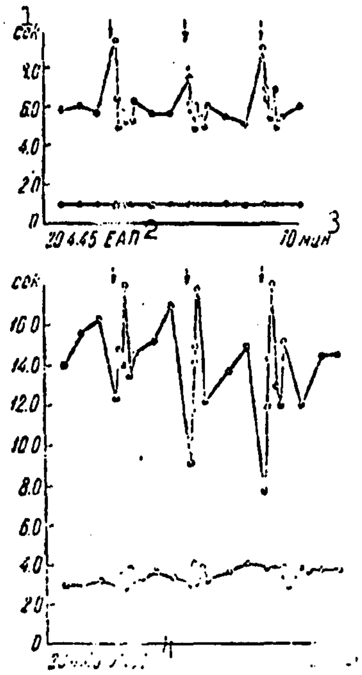

Fig. 8. Curves showing development and course of Purkinje visual afterimage against a background of vestibular, postrotational after reactions. Arrows indicate times at which subject was rotated. Other specifications the same as for Fig. 2. 1) Sec; 2) YeAP; 3) min; 4)LSD.

From this point of view, the study of the relationships between afferent systems both during active stimulation and afterwards, when after reactions and after-sensations develop, is interesting.

Actually, our experiments have shown that there are extremely essential relationships which arise during the interaction of after reactions and after-sensations in afferent systems of different modalities and within the visual system alone. We have been successful in proving that the course of the Hering image and the appearance of

three images in one eye depends on the functional state of the other eye. This dependence is expressed in terms of changes in the development time of the images and in the quality of their perception: the development time of the Hering image decreases; occasionally, the image disappears under the influence of stimulation of the other eye. When similar and complementary colors act on the other eye, the Hering image in the opposite eye is subject to opposed influences which take the form of an intensification or weakening of the colored component of the Hering image (experiments of 1940-1941). Very often, opposing, mutually exclusive effects on the colored and neutral components of the image are developed. If the colored component is intensified, this is accompanied by a weakening of the neutral component and vice versa; we are given the impression that antagonistic relationships exist between these components. Indeed, this does not always occur nor is it observed in all experiments. In addition, parallel changes in both components, proceeding in the same direction, occur and this is probably to be explained by a highly generalizing influence which encompasses the different levels of nervous organization of the afferent system. Moreover, when the Hering and Purkinje images develop simultaneously in one eye, the action of a light stimulus on the other eye causes an independent effect either on the Hering image or on the Purkinje image, a phenomenon which confirms the correctness of the concept of the fact that different levels of nervous organization effect these afterimages.

In experiments involving the influence of vestibular, postrotational after reactions and after-sensations (images) on the course of the Purkinje visual afterimage, definite and characteristic changes were noted in the latter (Fig. 8). The reaction to the cessation of rotation, which arises as a result of stimulation of the stopped semi-

circular canals, was accompanied in the majority of subjects by a decrease in the duration of the Purkinje image and by its distortion (movement) toward the side opposed to the sensation of counterrotation, independently of subjective perception of the reaction in the form of a sensation of counterrotation, which did not develop in all subjects (Fig. 8, LSD). In a minority of subjects, the reaction to the cessation of rotation conversely caused an increase in the duration of the Purkinje image and its distortion in the direction of prior rotation (Fig. 8, YeAP). After the cessation of the counterrotation reaction and after a certain quiescent interval, postrotational after reactions developed which, in the majority of subjects (but not always), was accompanied by the appearance of sensations of rotation or vestibular after-sensations, while in other subjects no after-sensations whatsoever arose. As a rule, the Purkinje image was subject to distortion (movement) to one side or the other and to changes in its duration and colored and neutral components (on the second-fifth determination after cessation of rotation) independently of the presence or absence of subjective perception of the postrotational after reactions: in certain subjects (LSD), the Purkinje visual image underwent a considerable increase in duration and color saturation during the vestibular after-sensation, while in others (YeAP), this phenomenon was less marked.

If, with Fischer and Wodak, we assume that vestibular after-sensations are independent of ocular nystagmus, it is necessary to acknowledge that their effects on the Purkinje visual afterimage is of intracentral character.

The table given above shows the cumulative results of experiments on the course of the Purkinje image against the background of the reaction to cessation of rotation and during the first and second ves-

1 Условия опыта	2 Вестибулярные реакции		5 Зрительный последовательный образ Пуркинье	
	3 ощущаемые, %	4 неощущаемые, %	6 смещенный, %	7 несмещенный, %
8 Реакция на прекращение вращения				
Контроль 9	45	55	96	4
Кофеин 10	40	60	100	—
Бензедрин 11	43	57	98	2
Стрихнин 12	25	75	99	1
13 Первый вестибулярный последовательный образ				
Контроль 9	9	91	51	49
Кофеин 10	23	77	65	35
Бензедрин 11	20	80	61	39
Стрихнин 12	5	95	67	33
14 Второй вестибулярный последовательный образ				
Контроль 9	7	[illegible]	[illegible]	55
Кофеин 10	6	[illegible]	42	58
Бензедрин 11	2	98	26	73
Стрихнин 12	2	98	30	70

1) Experimental conditions; 2) vestibular reactions; 3) perceived,%; 4) unperceived, %; 5) Purkinje visual afterimage; 6) distorted,%; 7) undistorted, %; 8) reaction to cessation of rotation; 9) control: 10) caffeine; 11) benzedrine; 12) strychnine; 13) first vestibular after-sensation; 14) second vestibular after-sensation.

tibular after-sensations (reactions), under experimental controlled conditions and after the administration of benzedrine, caffeine, and strychnine. It may be seen from the table that all three drugs, and strychnine in particular, decrease the number of subjectively perceived reactions to the cessation of rotation and it may be supposed that all of them increase the amount of distortion of the Purkinje visual afterimage. Caffeine and benzedrine produce twice the number of perceived vestibular after reactions as occur under the control conditions, while strychnine produces only approximately half as many; caffeine, benzedrine, and strychnine considerably increase the amount

of distortion (movement) of the Purkinje visual afterimage during the first vestibular after-sensation. This is less marked during the second vestibular after-sensation. These experiments of ours are in close correlation with the data obtained by Zagorul'ko, Komendantov, Osipova, and Entina (1944, 1947), who showed that changes occur in the development and course of vestibular after-sensations under conditions of low barometric pressure and under the influence of benzedrine. In the latter case, when the sensations consisted of a large number of phases, this number was reduced, when they consisted of a small number of phases, this number was increased, and in those subjects in whom these sensations were lacking under the control conditions, they now developed.

The monaural action of a sound is accompanied by a change in the functional state of the auditory afferent system, which has considerable influence on the course of the Hering visual afterimage; very often, the development time of the image is decreased and its brightness and size are increased; the first of these changes occurs during the second complex image in the appearance of the three Hering images and is quite often decolorized.

The development time of the Hering image is decreased three times as often during the auditory after-sensation as during the auditory stimulation, causing an increase in the decolorization of the second distorted image; the Hering image often increases in brightness and size. At the beginning and end of the auditory stimulation, the Hering image often disappears briefly. A change also occurs in the Hering image 6 minutes after cessation of the auditory after-sensations, whe there is no subjective perception of auditory after-sensations (experiments of 1940, 1941). Analogous data were obtained for the Purkinje image by Narikashvili (1944). Consequently, a substantial role in the

formation of visual afterimages is played by processes which occur in the lower, noncortical organization of the auditory afferent system and which are not subjectively perceived.

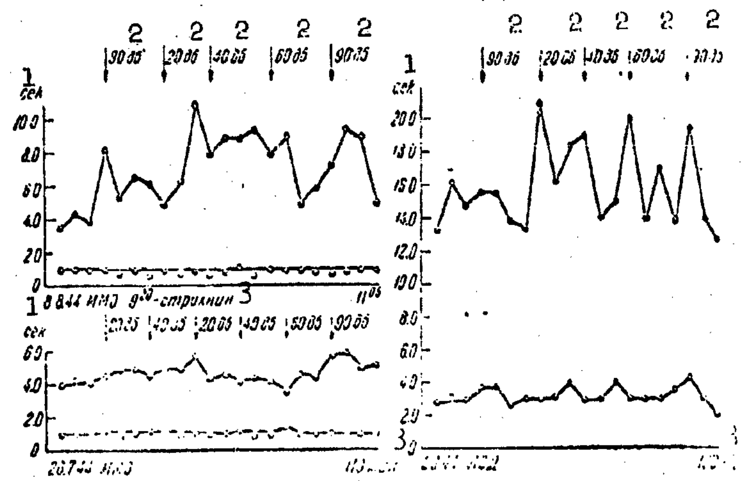

Fig. 9. Curves showing development and course of Purkinje afterimage during monaural stimulation (lower and right) of the ear, and the same after administration of strychnine (upper). Other specifications the same as for Fig. 2. 1) Sec; 2) db; 3) min; 4) LSD.

Our further experiments showed that there is a considerable change in the duration of the Purkinje image during stimulation of the auditory organ by sounds of different loudnesses (Fig. 9, LSD). The effect of auditory stimulation is intensified when the functional state of the central nervous system is altered by strychnine and caffeine (Fig. 9, MMC).

We cannot as yet precisely indicate the place where one afferent system acts directly on another, and in particular, we cannot show at which level of the intracentral pathways the interaction of the visual afferent system, on the one hand, and the auditory and labyrinthine systems, on the other hand, are effected. It is theoretically possible to assume that there are several levels of interaction. However, this

is undoubtedly nothing but the fact that the relationship between a subjectively perceived reaction (sensation) and an unperceived reaction is a different level of relationship than that which occurs when reactions of different afferent systems interact but are both subjectively perceived. In this respect, we may state some very general considerations. There is no doubt that, during the phylogenetic development of animals, culminating in man, there occurs an ever increasing degree of morphological complication and augmentation of different levels of nervous organization, each of which can effect phonoreactions, photoreactions, and vestibular reactions of greater or lesser complexity. It is precisely as a result of this that we cannot exclude the

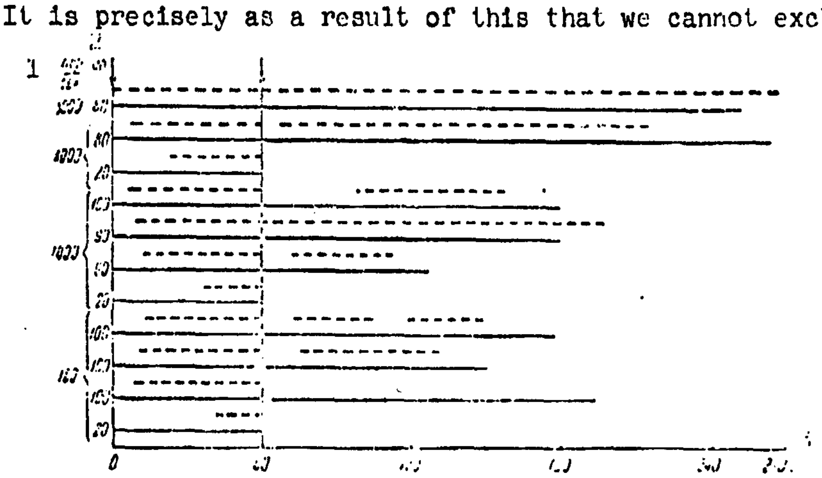

Fig. 10. Curves showing development and course of synesthetic visual sensations during monaural stimulation of the ear. Time in seconds is shown along the ordinate. The frequencies and loudnesses of the stimulatory sounds are shown at the left. The duration of the auditory stimulation is indicated (above) by arrows and was 60 seconds. The solid lines indicate auditory sensations and the dotted lines indicate visual sensations. 1) Cycles/sec; 2) db; 3) sec.

possibility of a multistage interaction between afferent systems. From L.A. Orbeli's point of view, the relationship between afferent systems can also occur at different levels of cortical centers, which are multistage structures.

It is no less difficult to discover the physiological mechanisms

governing the interaction between afferent systems.

The only demonstrable interaction of intracentral nature between afferent systems takes the form of synesthesia. The phenomenon of synesthesia consists in the fact that the response to an adequate stimulation of one sense organ consists not only in a sensation specific for that organ, but also in a second, accompanying sensation of another modality.

Fig. 10 shows the results of experiments in which the development of visual sensations was studied during monaural stimulation of the auditory system, as a function of the loudness and frequency of the stimulatory sound. The action of sonic frequencies from 100 to 10,000 cycles/second with loudnesses of from 10 to 100 db is accompanied by the development of visual sensations; these develop after a certain latent period, whose duration decreases as the loudness of the stimulatory sound increases. The visual sensations do not always disappear at the instant when sonic stimulation ceases, but continue through the development of the auditory after-sensation and even longer; one or two waves of visual sensations are observed and we designate these as synesthetic visual after-sensations (images).

In the experiments conducted by Kunstman and Orbeli (1923), both synesthesia and synkinesis arise as a result of disruption(or underdevelopment) of a composite, coordinational sensory or motor action when a certain section of a complex coordinational system does not play its proper role (or does not develop) and the balance of relationships between its individual sections is disrupted or when a system reacts with a specific activity in response to the reception of nonspecific excitation impulses at its centers. Under normal conditions of vital activity, we are subject neither to afterimages, nor synesthesia, nor synkinesis; nonspecific impulses of external origin are immediately

inhibited by the coordinational activity of the system. Consequently, we can, in this case, speak of irradiation of excitation from the centers of one afferent system to the centers of the other.

The interaction of afferent systems takes the form of antagonistic, reciprocal relationships and synergetic relationships. Furthermore, the processes of inductive relationships – simultaneous and sequential, positive and negative induction – may be based on the interaction of afferent systems. In addition, when sufficiently strong stimuli act on a sense organ, sympathetic innervation and, possibly, hormonal coordination are involved in the mechanism of interaction.

In any case, no matter how confined we may be by our point of view, the intracentral nature of the interaction of afferent systems remains indisputable.

It seems to us that the problem of the interaction of afferent systems which we have studied is also of importance in the pathophysiology of nervous and psychological diseases, where the study of the development and course of after reactions and afterimages (sensations) is a useful method of studying a pathological process, as L.A. Oberli (1939) has shown.

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